*J. Mar. Biol. Ass. U.K.* (1999), **79**, 479–486
Printed in the United Kingdom

# Diet of the European flying squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in the Balearic Sea (western Mediterranean)

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Stomach contents of *Todarodes sagittatus* caught by trawlers working from 100 to 800 m depth in the Balearic Sea (western Mediterranean) were studied. From the 348 stomachs examined (153 males and 195 females) 33.62% were empty (39.21% in males and 29.74% in females). The diet of the squid was composed of 58 different prey items belonging to four major groups: Osteichthya, Crustacea, Cephalopoda and Chondrichthya. Osteichthyes, crustaceans and cephalopods were the most common prey, with a frequency of occurrence value of 84.85, 48.92 and 29.87% respectively. A change in the diet as the squid grows was observed, since juveniles feed basically on fishes while adults prey more actively on crustaceans. Analysis of the diet by size-classes reflected an ontogenetic migration to deeper waters since, parallel to the increase of size, a raise in the percentage of prey species inhabiting deeper waters was detected. Cannibalism was quite frequent, since *T. sagittatus* was the second most common cephalopod prey. Females had higher fullness-weight index and lower emptiness index than males, which reflects their major energetic demand for egg production.

## INTRODUCTION

Stomach content analysis has demonstrated the important role played by cephalopods in marine food webs. As predators, they occupy high levels, preying on fishes, crustaceans and other cephalopod species (O'Dor, 1983; Castro & Guerra, 1990). On the other hand, cephalopods are preyed upon by fishes, birds and marine mammals (Hernández-García, 1995; Furness, 1994). The presence of hard structures resistants to digestive acids in cephalopods has facilitated the study of predator–prey relationships. Indeed, in the majority of cases the accurate analysis of cephalopod beaks allows the identification of the different species to which they belonged (Pérez-Gándaras, 1983; Clarke, 1986).

The diet of *Todarodes sagittatus* (Lamarck, 1798) has been studied in the north-east Atlantic (Jonsson, 1980; Wiborg & Gjøsæter, 1981; Wiborg et al., 1982; Wiborg & Beck, 1983; Breiby & Jobling, 1985; Sennikov & Bliznichenko, 1985; Sundet, 1985; Joy, 1990) and in the north-west African coast (Hernández-García, 1992). However, except Breiby & Jobling (1985), these studies treated the diet as part of a more general study concerning various aspects of the biology of this species or, as in Hernández-García (1992), dealt with the diet of other ommastrephid species. Moreover, all of them are incomplete studies as they refer to samples composed almost exclusively of immature individuals, where males are barely represented.

In the Atlantic Ocean *T. sagittatus* carry out an autumnal feeding migration from spawning areas to fishing grounds. These movements are basically constituted by immature females, which would explain the scarcity of males and mature females in the Atlantic samples. This migratory behaviour has not been observed in the Mediterranean Sea since the species is caught all year round (Quetglas et al., 1998). Despite the presence of a sedentary Mediterranean population, which permits the study of a complete life cycle, there are no studies of the diet of *T. sagittatus* in this area. Therefore, the present work is the first where the diet of all stages of *T. sagittatus* is analysed in Mediterranean waters.

## MATERIALS AND METHODS

Specimens were collected monthly from August 1995 to August 1996 onboard commercial trawlers off the ports of Andratx, Alcúdia and Palma (Figure 1). All the specimens were caught from 100 to 800 m depth in hauls performed during daytime hours (from 0800 to 1600 hours, approximately).

In the laboratory, the following measurements on fresh individuals were determined: mantle length (ML, to the nearest mm), total weight (TW, to the nearest 0.1 g), sex, digestive gland weight (DGW, to the nearest 0.01 g) and stomach weight (to the nearest 0.01 g). Size range of individuals analysed was from 8.1 to 30.7 cm ML in males and from 11.8 to 41.8 cm ML in females.

Stomachs were preserved in 70% ethyl alcohol until they were analysed. Prey were identified to the lowest possible taxon. Otoliths, beaks, scales, vertebrae and other hard parts were used to identify the stomach contents after comparison with a reference collection and published descriptions (Zariquiey-Alvarez, 1968; Pérez-Gándaras, 1983; Clarke, 1986).


**Figure 1.** Map of the study area: Majorca Island in the Balearic Sea (western Mediterranean).

The following indices were used for diet description and comparison: (i) frequency of occurrence (f), number of stomachs with a specific type of prey expressed as a percentage of the total number of stomachs containing food (Hyslop, 1980); (ii) numerical composition (Cn), total number of individuals of the same prey item expressed as a percentage of the total number of individuals in all food items (Hyslop, 1980); (iii) numerical importance (NI), calculated as $NI=\sqrt{f \cdot Cn}$ (Windell, 1968; Vesin et al., 1981); (iv) fullness–weight index (FWI), the weight of food in a digestive tract as a percentage of the body weight of the specimen (Cortez et al., 1995); (v) emptiness index (EMI), the percentage of specimens with no food in their stomachs (Cortez et al., 1995).

To determine if there were differences of diet with size, five length-classes were considered for males and females separately: $ML \leqslant 15$, $15 < ML \leqslant 20$, $20 < ML \leqslant 25$, $25 < ML \leqslant 30$ and $ML > 30$ cm (this last class comprised only females). In order to identify shifts in the diet composition with size, a cluster analysis on the frequency of occurrence of the prey groups cited below was performed. The Spearman correlation coefficient was used for the similarity index, and the unweighted-pair method using arithmetic averages (UPGMA) was used for the aggregation algorithm.

This work was carried out in the framework of a project concerning the study of the bottom trawl fisheries from the western Mediterranean. In that project, three depth strata were established: (A) from 50 to 150 m; (B) from 150 to 350 m; and (C) >350 m. In the present study, in order to give ecological sense to the prey groups considered, teleosts found in the stomach contents were classified according to whether their major frequency of appearance was in stratum B or C (Carbonell et al., 1997). Thus, to perform the cluster analysis the following prey groups were considered: Isopoda, Decapoda: Natantia, Decapoda: Reptantia, Cephalopoda, Chondrichthya, Osteichthya B and Osteichthya C (unidentified teleosts were not considered).

The individuals sampled in this study had been the object of a previous work concerning biological aspects of the species; the depth range was divided in accordance with the bathymetric distribution of the fishing grounds in which the trawlers worked: <100, 100–200, 200–400 and 600–800 m. In order to determine the relationship between the diet and the stratum inhabited, the percentage of appearance for each size-class at each stratum was calculated (Quetglas et al., 1998). The condition index (CI), defined as the percentage between the digestive gland weight and total body weight (less digestive gland weight), was used as an indicator of condition (Joy, 1990).

The FWI and the CI showed no normal distribution (Kolmogorov–Smirnov test, $P<0.01$) being compared consequently by the Kruskal–Wallis test, followed by a multiple comparison test (Siegel & Castellan, 1988). The EMI was tested by the Fisher exact test (Zar, 1984) between sexes of the same size and between succesive sizes for each sex. A significance level of $P=0.05$ was considered.

To analyse the selectivity of *Todarodes sagittatus* as a predator, the relationship between the size of cephalopod

**Table 1.** *Indices used to quantify the diet of* Todarodes sagittatus*: frequency of occurrence (f), numerical composition (Cn) and numerical importance (NI). For osteichthyans the depth stratum in which they occurred is indicated between parentheses.*

| Prey category | f (%) | Cn (%) | NI (%) |
|---|---|---|---|
| Crustacea | 48.92 | 21.21 | 32.21 |
| Isopoda | 3.03 | 1.25 | 1.94 |
| Decapoda Natantia | 42.42 | 18.54 | 28.04 |
| *Alpheus glaber* | 0.43 | 0.18 | 0.28 |
| *Aristeus antennatus* | 6.06 | 2.50 | 3.89 |
| *Crangonidae indeterminate* | 0.87 | 0.36 | 0.56 |
| *Pasiphaea multidentata* | 0.87 | 0.36 | 0.56 |
| *Pasiphaea sivado* | 0.43 | 0.18 | 0.28 |
| *Pasiphaea* sp. | 1.73 | 0.89 | 1.24 |
| *Plesionika giglioli* | 1.73 | 1.07 | 1.36 |
| *Plesionika heterocarpus* | 3.03 | 1.25 | 1.94 |
| *Plesionika* sp. | 0.87 | 0.36 | 0.56 |
| *Processa canaliculata* | 0.43 | 0.18 | 0.28 |
| *Processa* sp. | 0.43 | 0.18 | 0.28 |
| Natantia unidentified | 26.4 | 111.05 | 17.08 |
| Decapoda Reptantia | 3.46 | 1.43 | 2.22 |
| *Nephrops norvegicus* | 0.43 | 0.18 | 0.28 |
| *Munida* sp. | 0.43 | 0.18 | 0.28 |
| *Munida iris* | 1.73 | 0.71 | 1.11 |
| *Medaeus couchi* | 0.87 | 0.36 | 0.56 |
| Cephalopoda | 29.87 | 17.83 | 23.07 |
| *Ancistroteuthis lichtensteini* | 0.87 | 0.53 | 0.68 |
| *Bathypolipus sponsalis* | 0.87 | 0.36 | 0.56 |
| *Heteroteuthis dispar* | 1.73 | 1.07 | 1.36 |
| *Histioteuthis bonnellii* | 0.43 | 0.18 | 0.28 |
| *Histioteuthis reversa* | 2.16 | 0.89 | 1.39 |
| *Illex coindetii* | 0.43 | 0.18 | 0.28 |
| *Loligo forbesi* | 0.43 | 0.53 | 0.48 |
| *Neorossia caroli* | 0.43 | 0.18 | 0.28 |
| *Onychoteuthis banksi* | 2.60 | 1.07 | 1.67 |
| *Sepietta neglecta* | 0.43 | 0.18 | 0.28 |
| Sepiolidae unidentified | 6.06 | 5.53 | 5.79 |
| *Thysanoteuthis rhombus* | 0.87 | 0.36 | 0.56 |
| *Todarodes sagittatus* | 4.76 | 2.14 | 3.19 |
| Cephalopoda unidentified | 10.82 | 4.63 | 7.08 |
| Chondrichthya | 2.60 | 1.07 | 1.67 |
| *Galeus melastomus* | 1.30 | 0.53 | 0.83 |
| Chondrichthya unidentified | 1.30 | 0.53 | 0.83 |
| Osteichthya | 84.85 | 59.36 | 70.97 |
| *Argyropelecus hemigymnus* (C) | 1.30 | 0.53 | 0.83 |
| *Boops boops* (B) | 0.87 | 0.36 | 0.56 |
| Clupeidae unidentified (B) | 0.43 | 0.18 | 0.28 |
| *Chauliodus sloani* (C) | 3.46 | 1.43 | 2.22 |
| *Glossanodon leioglossus* (B) | 3.90 | 1.60 | 2.50 |
| *Lepidopus caudatus* (B) | 19.05 | 14.62 | 16.69 |
| *Maurolicus muelleri* (C) | 3.03 | 1.43 | 2.08 |
| *Nezumia aequalis* (C) | 0.43 | 0.18 | 0.28 |
| *Notolepis rissoi* (C) | 6.06 | 3.21 | 4.41 |
| *Polyacanthonotus rissoanus* (C) | 0.43 | 0.18 | 0.28 |
| *tomias boa* (C) | 4.33 | 1.78 | 2.78 |
| *Centracanthus cirrus* (B) | 0.43 | 0.18 | 0.28 |
| *Spicara smaris* (B) | 0.43 | 0.18 | 0.28 |
| *Benthosema glaciale* (C) | 1.30 | 0.89 | 1.08 |
| *Ceratoscopelus maderensis* (C) | 8.66 | 4.46 | 6.21 |
| *Hygophum hygomi* (C) | 1.30 | 0.53 | 0.83 |
| *Lampanyctus crocodilus* (C) | 2.16 | 0.89 | 1.39 |
| *Notoscopelus elongatus* (C) | 1.30 | 0.53 | 0.83 |
| *Symbolophorus veranyi* (C) | 0.43 | 0.18 | 0.28 |
| *Merluccius merluccius* (B) | 0.43 | 0.18 | 0.28 |
| *Micromesistius poutassou* (C) | 3.03 | 1.25 | 1.94 |
| *Lepidion lepidion* (C) | 0.43 | 0.18 | 0.28 |
| *Mora moro* (C) | 0.43 | 0.18 | 0.28 |
| Osteichthya unidentified | 43.29 | 24.24 | 32.40 |
| Plastic | 0.87 | 0.36 | 0.56 |

prey and the predator size was determined, and a linear regression analysis was posteriorly calculated. The mantle length of the cephalopods was estimated from beak measurements using the relationships proposed by Würtz et al. (1992) for *Ancistroteuthis lichtensteini* and *Histioteuthis reversa*, Quetglas et al. (1998) for *T. sagittatus* and Clarke (1986) for the rest of species.

## RESULTS

From the 348 individuals examined (153 males and 195 females) 33.62% of stomachs were empty (39.21% in males and 29.74% in females). Table 1 shows the values of the indices used to quantify the diet of *Todarodes sagittatus*, which was composed of 58 different prey items belonging to four major groups (Crustacea, Cephalopoda, Chondrichthya and Osteichthya).

For males, the percentage of stomachs containing one or two types of prey was very similar (38.71% and 37.63%, respectively), 19.35% contained three, 4.3% four and there were no stomachs with more than four types of prey. For females, one type was present in 40.88% of the stomachs, 30.66% contained two, 19.71% three, 7.30% four and 1.46% contained more than four types of prey.

### *Prey spectrum*

Osteichthyes was the most common prey appearing in 84.85% of the stomachs and with a numerical importance value of 70.97%. The most common species was *Lepidopus caudatus* followed by *Ceratoscopelus maderensis* and *Notolepis rissoi*. However, the values concerning the first species are possibly overestimated because they come from an unusual haul, where a large number of squid pursuing a shoal of *L. caudatus* were caught. Crustaceans constituted the second most important group, with frequency of occurrence and numerical importance values of 48.92% and 32.21%, respectively. Among crustaceans, the Decapoda: Natantia predominated (f=42.42% and NI=28.04%), the red shrimp, *Aristeus antennatus*, being the most common species. Cephalopods also constituted an important group of prey (f=29.87% and NI=23.07%) and cannibalism occured frequently, since *T. sagittatus* appeared in 4.76% of the stomachs containing food. Finally, the diet of the species studied was completed by isopods (f=3.03%, NI=1.94%) and chondrichthyes (f=2.60%, NI=1.67%).

The frequency of occurrence values by sex and class size are shown in Figure 2. The importance of osteichthyes clearly decreases with size: from 64.29% in males of ML<15 cm to 48.64% in those of 25<ML<30 and from 76.92% to 47.31% in females of ML<15 cm and ML>30 cm, respectively. Among these teleosts, exists a decrease of osteichthyes B with size (from 14.29 to 2.70% in males and from 30.77 to 6.45% in females) associated to an increase of osteichthyes C (clearer in males than in females). The importance of Decapoda Natantia also increases with size, going from 7.14 to 37.84% in males and from 17.86% in females of 15<ML<20 cm (it did not appear in those smaller than 15 cm ML) to 31.11% in females of ML>30 cm. The importance of cephalopods clearly decreases in males



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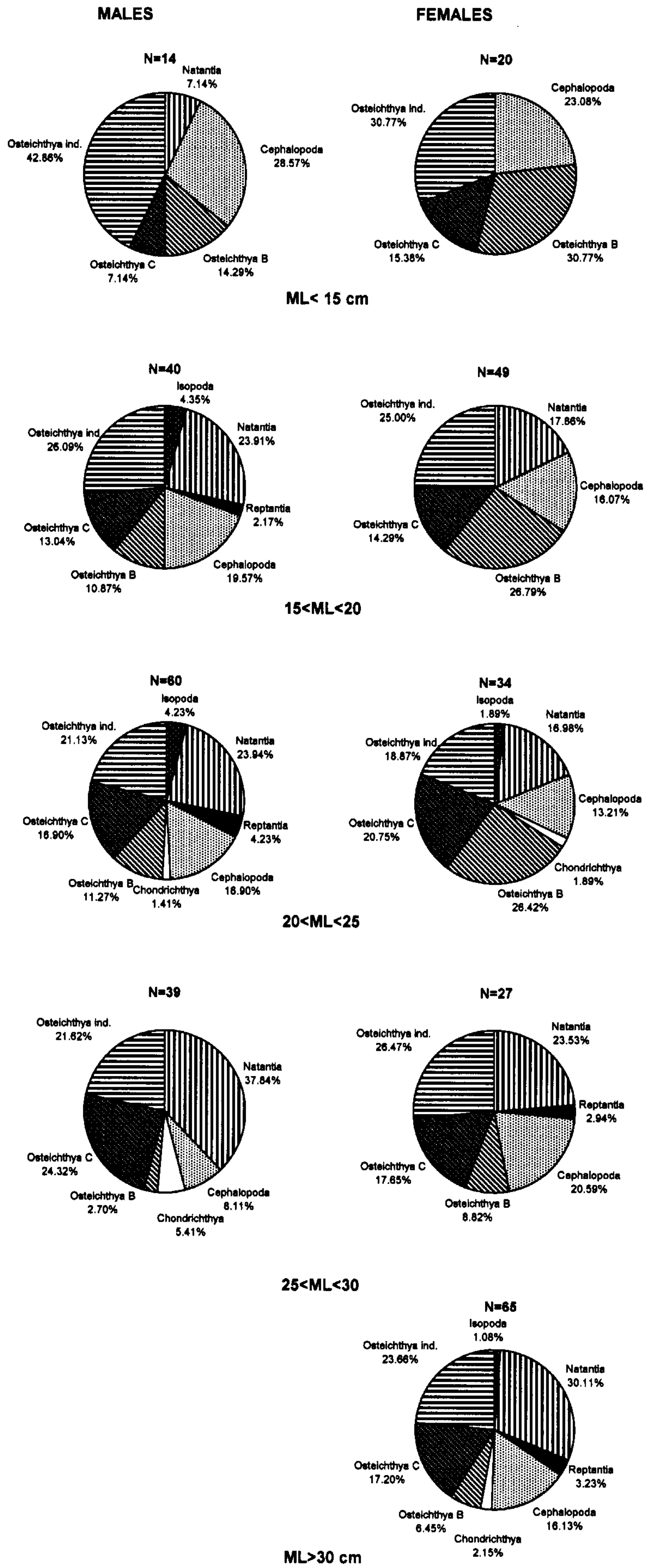


**Figure 2.** Frequency of occurrence values by sex and size-class of the different prey items found in the stomach contents.



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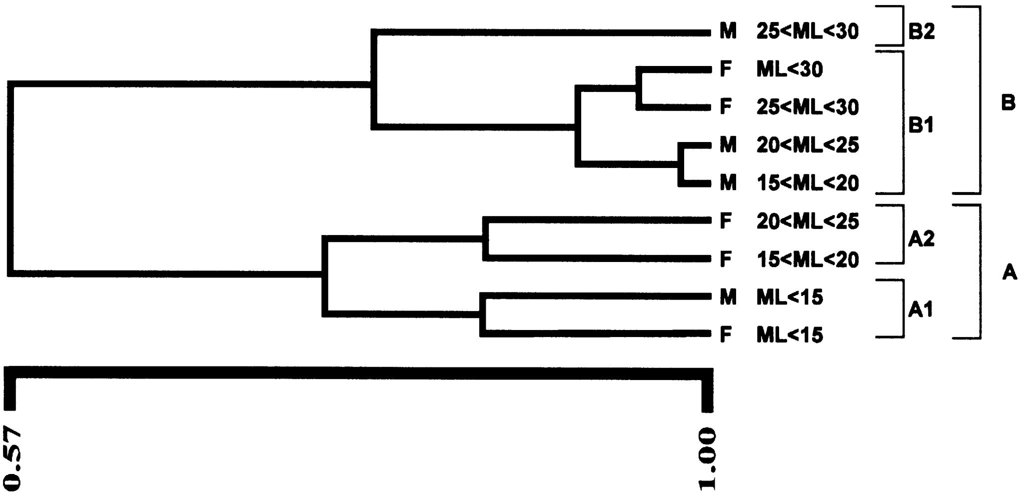


**Figure 3.** Results of the cluster analysis on the frequency of occurrence values of the different prey items (excluding unidentified osteichthyes).

(from 28.57 to 8.11%) but this diminution (as in the case of osteichthyes C) is not so clear in females.

### *Cluster analysis*

Two main groups of size-classes were identified by cluster analysis (Figure 3): females smaller than 25 cm ML and males smaller than 15 cm ML constituted the group A, being the group B represented by females from 25 cm ML and males from 15 cm ML. These two principal groups can be further divided into various subgroups. Group A was constituted by males and females smaller than 15 cm ML (subgroup A1) and females from 15 to 25 cm ML (subgroup A2). On the other hand, group B was also subdivided into two subgroups: males from 15 to 25 cm ML and females larger than 25 cm ML constituted the subgroup B1 while males from 25 to 30 cm ML formed the subgroup B2.

Group A is characterized by the high values of osteichthyes B (from 14.29 to 30.77%) and low percentages of crustaceans Natantia (from non-existent to 17.86%). The separation between subgroup A1 and A2 can be due to the higher percentage of cephalopods in the former (28.57 and 23.08% vs 16.07 and 13.21%) and to the major importance of natantia in subgroup A2. Group B is characterized for high values of Natantia (from 23.53 to 37.84%) and low values of osteichthyes B (from 2.70 to 11.27%). Subgroup B1 and B2 are only separated by the different percentages of osteichthyes B (10.87 and 11.27% vs 8.82 and 6.45%) because values for the other prey types are very similar. The subgroup B3 has the greatest values of Natantia, osteichthyes C and chondrichthyes of all the size-classes (37.84, 24.32 and 5.41%, respectively) and also the lowest percentage of cephalopods (8.11%).

**Table 2.** *The percentage of appearance of each size-class at each depth stratum for males (A) and females (B).*

*A. Males*

| Size (cm) | Depth strata (m) 100–200 | 200–400 | 400–600 | 600–800 |
|---|---|---|---|---|
| ML < 15 | 42.86 | 28.57 | 14.29 | 14.29 |
| 15 < ML < 20 | 17.50 | 17.50 | 47.50 | 17.50 |
| 20 < ML < 25 | 0.00 | 13.56 | 57.63 | 28.81 |
| 25 < ML < 30 | 0.00 | 0.00 | 28.57 | 71.43 |

*B. Females*

| Size (cm) | Depth strata (m) 100–200 | 200–400 | 400–600 | 600–800 |
|---|---|---|---|---|
| ML < 15 | 60.00 | 40.00 | 0.00 | 0.00 |
| 15 < ML < 20 | 22.45 | 51.02 | 20.41 | 6.12 |
| 20 < ML < 25 | 2.94 | 47.06 | 26.47 | 23.53 |
| 25 < ML < 30 | 0.00 | 12.50 | 41.67 | 45.83 |
| ML > 30 | 0.00 | 1.64 | 44.26 | 54.10 |

The percentage of appearance of each size-class at each depth stratum is shown in Table 2. Group B determined by the clustering would inhabit mainly the deeper strata (from 400 to 800 m) while group A would appear in shallower waters but in a wide range, from 100 to 600 m. Individuals of ML < 15 (subgroup A1) appeared mainly from 100 to 400 m and females from 15 to 25 cm ML (subgroup A2), although more disperse, inhabited mainly the 200–600 m depth range. Males from 15 to 25 cm ML and females from 25 cm ML (subgroup B1) were more frequent in the 400–800 m while males of 25 < ML < 30 (subgroup B2) appeared mainly in the 600–800 m stratum.

### *Indices*

The evolution of FWI, EMI and CI in relation to size-classes is represented in Figure 4. The Kruskal–Wallis test between all groups showed significant differences for FWI and CI ($P<0.0001$ in both cases). Fullness–weight index decreased progressively with size and differences were found between sexes of the same size for the size ranges 15 < ML < 20 cm and 20 < ML < 25 cm and between females of 25 < ML < 30 cm and ML > 30 cm ($P<0.05$). Condition index also decreased with size except for females of ML > 30 cm, and significant differences were found between sexes of the same size



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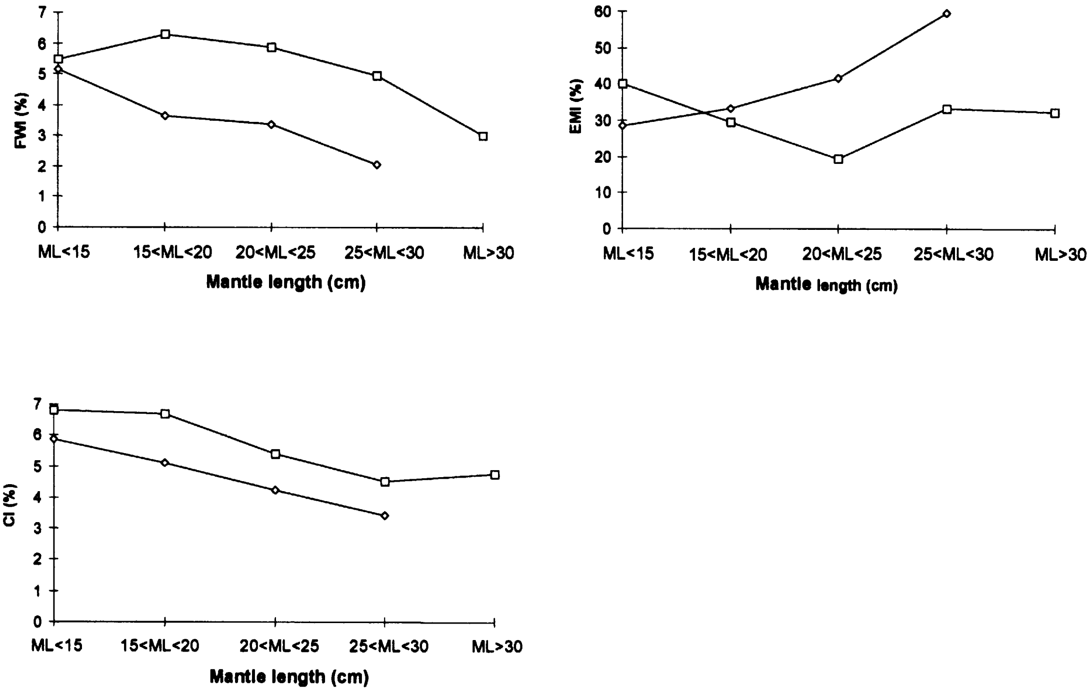


**Figure 4.** Evolution of fullness–weight index (FWI) (A), emptiness index (EMI) (B) and condition index (CI) (C) in relation to size-class, for males (◇) and females (□).

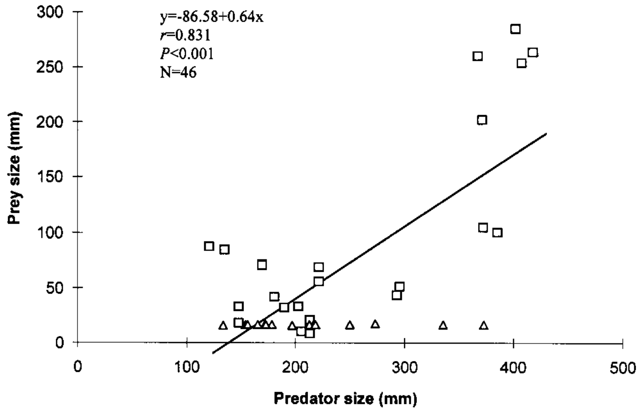


**Figure 5.** Relationships between cephalopod prey size and predator size. △, sepiolids; □, rest of the cephalopod species.

for individuals of 15 < ML < 20 cm and 20 < ML < 25 cm and between females of 15 < ML < 20 cm and 20 < ML < 25 cm ($P$ < 0.05). Emptiness index showed only differences between males and females of 20 < ML < 25 cm ($P$ < 0.05). For males, the EMI increased gradually with size, while for females it decreased from individuals of ML < 15 cm to 20 < ML < 25 cm, before increasing and maintaining constant values for those of 25 < ML < 30 cm and ML > 30 cm.

### *Predator–prey relationships*

Figure 5 shows the relationship between cephalopod prey size and predator size. There is a clear increase of prey size with the enlargement of predator size, much clearer if sepiolids are not taken into account. Larger individuals feed mainly on larger prey but also on a wide range of prey sizes. It has been observed that squid larger than 30 cm ML, although they tend to prey on larger sizes, can also eat small species like sepiolids.

## DISCUSSION

The majority of cephalopods are carnivores preying on a wide variety of prey (Nixon, 1987). Such a versatile diet is consistent with the general view of cephalopods as opportunistic predators and proves how adaptable they are (Summers, 1983). Prey spectrum in the diet is related to the most readily available prey (Boyle, 1990) and it can be observed that, in general, pelagic species tend to prey mainly on fishes while crustaceans predominate in the benthic species (Castro & Guerra, 1990; Cortez et al., 1995; Coelho et al., 1997).

Results of the present study confirm the predominance of fish in the diet of *Todarodes sagittatus*, as was observed by earlier researchers (Wiborg & Gjøsæter, 1981; Wiborg et al., 1982; Sennikov & Bliznichenko, 1985; Sundet, 1985; Breiby & Jobling, 1985; Joy, 1990). Also in accordance with these authors, with the exception of Sennikov & Bliznichenko (1985) and Joy (1990), crustaceans were more frequent than cephalopods in the stomach contents. The same prey items have been found in other species of the same genera, such as *T. angolensis* (Sánchez, 1982) and *T. pacificus* (Okutani, 1962).

With respect to the type of prey, there exists general agreement that *T. sagittatus* feeds mainly on pelagic organisms. Stomach contents analysed in the present work also revealed pelagic species, either fishes (myctophids, *Lepidopus caudatus*, *Notolepis rissoi*, *Glossanodon leioglossus*, *Chauliodus sloani*, *Micromesistius poutassou*), crustaceans (*Plesionika* spp., *Aristeus antennatus*, *Pasiphaea* spp.) or cephalopods (ommastrephids, *Histioteuthis* spp., *Onychoteuthis banksi*, *Ancystroteuthis lichtensteini*). However, and as previously reported by Jonsson (1980), *T. sagittatus* may also eat benthic prey as revealed by the presence of these species in our samples (crustaceans Reptantia, *Bathypolipus sponsalis*, *Galeus melastomus*). In daytime, the species has been observed near the bottom (Moiseev, 1991) what would explain the presence of benthic species in the diet.

In the majority of cephalopod species the existence of ontogenetic shifts in the diet has been reported (Coelho et al., 1997). Apart from widening their prey spectrum as they grow, it is observed that adults feed mainly on fish and cephalopods while juveniles base their diet on crustaceans (Nixon, 1987). Although our results show an increase of the number of prey types with size, the change from crustaceans to fish and cephalopods was not observed. On the contrary, and in disagreement with Breiby & Jobling (1985), the importance of fishes and cephalopods decreases with size, while the percentage of crustaceans increase. The results obtained show that the prey spectrum found in the different size-classes reflects the ontogenetic migration to deeper waters observed by Quetglas et al. (1998). With the increase of size, there appears a progressive increase of species inhabiting deep waters (Natantia and osteichthyes C) associated with a decrease in species from shallower waters (osteichthyes B).

The diminution of FWI with size in both sexes would be related to the decrease of metabolic rate with growth (O'Dor & Wells, 1987). Females had higher FWI and lower EMI values than males, which could reflect their major energetic demand for egg production, as observed in other cephalopod species (Castro & Guerra, 1990; Cortez et al., 1995).

Condition index values were clearly lower than those found in the Atlantic ocean by earlier studies (Wiborg & Gjøsæter, 1981; Wiborg et al., 1982; Joy, 1990) and, in disagreement with Joy (1990), the index decreased with size in both sexes. The increase of CI observed in Atlantic waters, where a feeding migration occurs, suggested intensive feeding activity leading to a rapid absorption and storage of energy within the digestive gland (Joy, 1990).

Nothing can be said about daily rhythms of feeding activity because all specimens were caught in daytime hours, but Shimko (1984) and Hernández-García (1992) found that the highest stomach fullness values were registered at night and Shimko (1984) also observed a relationship between the phases of the moon and feeding activity.

In relation to size selectivity in the diet of *T. sagittatus*, it was observed that larger individuals preyed on larger prey sizes but also in a wider range of sizes, as was pointed out in other species (Collins & Pierce, 1996; Rasero et al., 1996). These authors obtained an increase in the size of prey consumed up to a determined size of the predator, after which no further increase in prey size was detected. This phenomenon could be due to the fact that when squid take large fishes they consume only flesh, rejecting hard structures to be analysed the prey size (Breiby & Jobling, 1981; Rasero et al., 1996).

Cannibalism in *T. sagittatus* was supposed to be an artefact of the fishing technique by earlier authors (Wiborg & Gjøsæter, 1981; Breiby & Jobling, 1985; Sundet, 1985). In this study, however, the low number of individuals caught in each haul (Quetglas et al., 1998) and the elevated degree of digestion of squid remains suggested that cannibalism was a natural behaviour. Cannibalism in *T. sagittatus* would be rather important, since in the present work it was the most frequent cephalopod prey after sepiolids. Sennikov & Bliznichenko (1985) consider cannibalism in this species of great importance during periods of poor food supply.

This study was carried out within the framework of the project 'Discards of the western Mediterranean trawl fleets' (Contract ref. DG-XIV, MED/94/027). We wish to express our gratitude to the crew of the trawlers 'Illa del Sol', 'Nou Capdepera', 'Portocolom' and 'Rafael Irene' for their kindness during the on-board sampling. We would also like to thank Dr Enric Massutí and Joan Moranta for their useful comments, Ramon Alemany for the technical assistance in edition processing and Sandra M. Starbuck for the English version.

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*Submitted 16 July 1998. Accepted 5 October 1998.*